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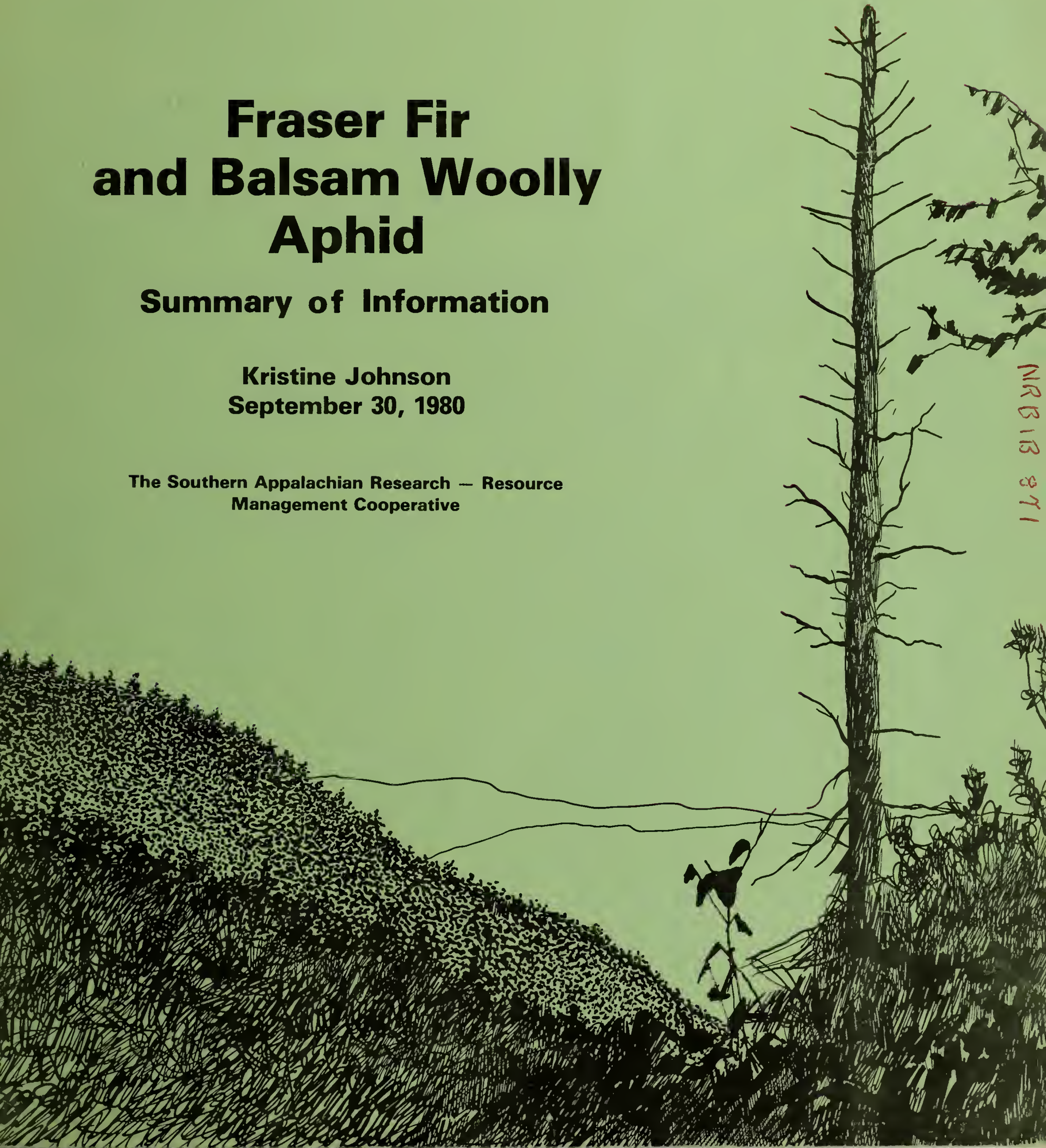
Fraser Fir and Balsam Woolly Aphid

Summary of Information

Kristine Johnson
September 30, 1980

The Southern Appalachian Research — Resource
Management Cooperative



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FRASER FIR AND THE BALSAM WOOLLY APHID

SUMMARY OF INFORMATION

BY

KRISTINE D. JOHNSON

SEPTEMBER 30, 1980

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Foreward

In April, 1980, the Fraser Fir/Balsam Woolly Aphid Technical Committee of the Southern Appalachian Research/Resource Management Cooperative (SARRMC) sponsored a conference at Crossnore, North Carolina. Those attending exchanged information and ideas during three workshops dealing with different aspects of the balsam woolly aphid problem--status of Fraser fir as a species, short term management and protection and long term management protection.

Following the conference, the Technical Committee decided to sponsor the preparation of this report which summarizes current information on both the host and pest. Its format corresponds with that of the conference workshops to facilitate reference to the conference Problem Analysis and Proceedings. The first section provides botanical and ecological descriptions of the host, Fraser fir. Its commercial use is also discussed, along with its legal status with respect to the Endangered Species Act, Plant Pest Laws and other relevant legislation. The second section outlines each agency responsible for management of Fraser fir forests, including a brief statement of general policy, a history of the balsam woolly aphid in areas under their administration and efforts to deal with the problem. Issues relating to protection of present fir stands and continuing seed supply are also discussed. The third section presents a review of research dealing with impact assessment, the biology of the balsam woolly aphid and host-pest interactions.

Much of the information for this report was obtained in a thorough review of scientific literature. Interviews, correspondence and conversation with individual researchers and representatives of federal and

state agencies were also valuable sources. Appreciation is extended to all those who shared their knowledge and ideas. The Technical Committee of SARRMC - Dr. Ron Hay of the University of Tennessee, Pat Barry of the U.S. Forest Service and Dr. Jim McGraw of the North Carolina Agricultural Extension Service--and the Executive Director, Dr. John McCrone of Western Carolina University, provided guidance throughout the project and reviewed the final manuscript. Christopher Eagar and Dr. Eyvind Thor, both of the University of Tennessee, also assisted with suggestions and criticism. Bibliographic material was shared by Dr. Hugh Schooley and Dr. George Puritch, both of the Canadian Forestry Service, Dr. Garrett Smathers of Western Carolina University and Dr. Fred Hain of North Carolina State University. Dr. Gerry Fedde and Dr. Gene Amman, both of the U.S. Forest Service, supplied unpublished research information. Many questions were answered by Thomas Rhyne of the North Carolina Division of Forest Resources, Bryan Taylor of the North Carolina Division of Parks and Recreation, Howard Singletary, Plant Pest Administrator for the North Carolina Department of Agriculture and Kirby Brock of the U.S. Forest Service. Finally, Hoover Lambert of the U.S. Forest Service deserves special recognition for his interest in this project as well as for years of dedicated work with the balsam woolly aphid.

Funding for this report was provided through SARRMC by the U.S. Forest Service, Southeastern Area State and Private Forestry--Forest Insect and Disease Management, Field Supervisor Harold Flake. Use of facilities at the University of Tennessee Department of Forestry, Wildlife and Fisheries was co-ordinated by Dr. Ron Hay, and the manuscript was typed by Betty Perrin and Marilyn Hamilton.

INTRODUCTION

The balsam woolly aphid (Adelges piceae [Ratz.]) originated in Europe, probably as a derivative of the closely related A. nusslini (Borner), where it was a relatively innocuous pest on European silver fir (Abies alba [L.] Mill.). Its history on the North American continent is similar to that of several other disastrous plant pests: introduced accidentally on nursery stock, the woolly aphid thrived and spread so rapidly that it was already well established on balsam fir (Abies balsamea [L.] Mill.) in Maine and Maritime Canada before official identification was made in 1908. Damage to this commercially important fir has been extensive and occasionally severe all over the northeast. A separate introduction from Europe put the woolly aphid into the Pacific Northwest, where it first appeared around 1930.

In 1957 the insect was first identified in the Southern Appalachian Mountains on Mt. Mitchell, North Carolina, on Fraser fir (Abies fraseri [Pursh.] Poir.). Its subsequent spread throughout the range of the host in the Southern Appalachians was facilitated by the extreme susceptibility of Fraser fir as well as the remarkable reproductive and dispersal capabilities of the balsam woolly aphid. Extensive fir mortality has occurred in all areas except Mt. Rogers, Virginia, where infestations dating back to the mid-1960's were first discovered in 1979.

Fraser fir is of scenic and scientific value as a major component of the spruce-fir ecosystem; it also has commercial importance as a Christmas tree. Its potential loss has caused concern among scientists and forest resource managers in the Southern Appalachian region, and

in the past twenty years considerable contributions have been made to balsam woolly aphid research. The purpose of this report is to provide a summary of current information on the problem of the balsam woolly aphid in this region, with particular emphasis on implications for the legal and biological status of Fraser fir and its management and protection.

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STATUS OF THE SPECIES

Botanical Description

Fraser fir (Abies fraseri [Pursh.] Poir.) is the only fir endemic to the Southern Appalachian mountains. Its leaves are linear, flattened, dark shiny green above and silvery banded below; cones are oblong and green tinged with purple. The stem of Fraser fir is composed of a series of internodes produced in successive growing seasons. On healthy young trees the bark surface is smooth along internodes and roughened at nodes by bark folds. Internodal bark surface is interrupted by lenticels, needle scars and numerous small swellings or "blisters" which contain clear liquid resin. Bark fissures and scales develop on the lower portion of the stem and become more widespread with maturity or reduced vigor. Bark on mature trees is seldom thicker than 1.8 cm near the stump (Bryant, 1976). Fraser firs typically live 150 years and attain a height of 25 meters and a diameter of 50 centimeters.

Taxonomy

Fraser fir belongs to a close related group which also includes balsam fir (A. balsamea [L.] Mill.) and subalpine fir (A. lasiocarpa [Hook.] Nutt.). Most taxonomists consider each as separate on the species level. Fraser fir, however, was once known as A. balsamea var. fraseri and some question remains concerning its proper taxonomic designation. Balsam fir is found from Canada south into the mountains of northern Virginia and is replaced by Fraser fir in the mountains of southwestern Virginia, eastern Tennessee and western North Carolina.

Bracted balsam fir (A. balsamea var. phanerolepis Fern.) is recognized as an intermediate in range and certain characteristics between the two species.

Fraser and balsam fir are generally distinguished on basis of the number of hypodermal cells that may be counted in the cross section of a needle and the bract-to-scale ratio on cones. Fraser fir has a greater hypodermal cell count than balsam fir and the bract is longer than the cone scale, sharply recurved and protrudes outside the cone, while on balsam fir the bract is shorter and hidden beneath the cone scale (Robinson and Thor, 1969). Chemical and quantitative taxonomic methods have recently been used to explore geographic variability in the relationships between these species. Analysis of monoterpenes in the bark showed a low variability in characteristics for Fraser fir, indicating a reduction in the gene pool (Zavarin and Snajberk, 1972). Thor and Barnett (1974) also used monoterpene analysis to determine that bracted balsam fir, while intermediate in selected characteristics, is not of hybrid origin since it had no greater variation than either putative parental population. The monoterpene data, as well as morphological characteristics, indicate a geographic variation pattern with relatively gradual changes in a north-south direction. This evidence, along with similar findings by Myers and Bormann (1963), substantiates the theory that the eastern firs are remnants of a once-continuous population. During the Pleistocene glaciation the boreal forests extended much further than their present range, but as the climate warmed the southern firs were replaced at the lower elevation by species better adapted to a warm environment (Whittaker, 1956).

At the present balsam fir has a larger range and greater variety of habitat--with a correspondingly larger gene pool--than the Fraser fir on isolated southern mountain tops. Thor and Barnett (1974) state that while continued isolation and selection pressure may eventually result in significant differences between them, there is presently no reason to recognize Fraser fir as more than a variety of balsam fir. This issue, however, may never be completely resolved since taxonomic distinctions between strong varities and real species are basically arbitrary and liable to depend on the custom or philosophy of individual botanists. The same is true of the designations "variety" and "subspecies."

Ecology

Fraser fir and red spruce (*Picea rubens* Sarg.) are the major components of the spruce-fir forest type, which occurs in a disjunct pattern in the Southern Appalachians at elevations above 1,280 meters. The mixture of spruce and fir varies primarily with elevation, although disturbance and other site factors may also be important. In mature communities red spruce is dominant in the canopy at elevations between 1,280 meters and 1,700 meters, with fir restricted to intermediate and occasionally codominant crown class status. Between 1,700 meters and 1,830 meters the mixture becomes more equal, though spruce decreases in importance in size and stem frequency toward the upper limits of this elevational segment. Above 1,830 meters Fraser fir occurs in virtually pure stands (Whittaker, 1956). Commonly associated canopy trees include *Sorbus americana*, *Prunus pennsylvanica*, *Betula lutea* and *Acer spicatum*; shrubs include *Acer pennsylvanicum*, *Vaccinium erythrocarpum*, *Viburnum*

alnifolium, Rhododendron catawbiense and Rhododendron maximum. Isolated spruce and fir trees also occur on grassy balds and other open areas.

Red spruce attains a larger size and lives longer than Fraser fir, but the latter grows more rapidly and produces more prolific seed crops. Oosting and Billings (1951) found that Fraser fir was three to five times more abundant in spruce-fir stands than red spruce (including both seedlings and trees), although spruce had a greater basal area. Both species are highly shade tolerant and thus able to regenerate under an existing canopy, and both respond well to release. Red spruce trees have exceptionally slow-growing, fibrous, shallow root systems, and their establishment is suppressed by thick litter layers where susceptibility to drying is high. In contrast, the roots of Fraser fir are deeper and grow more rapidly, providing an adaptive advantage in open areas where the upper inch or so of soil is dried by sun and wind. Fraser fir thus plays an important role as a pioneer species, occupying openings with dense, vigorous reproduction.

Commercial Use

The original spruce-fir forests of the Southern Appalachians covered around 800,000 hectares (2,000,000 acres). Clearing for agriculture and minor logging had reduced the size to 300,000 hectares (750,000 acres) by the time of the Civil War (Hopkins, 1889). During the following 80 years the spruce-fir forests were exploited extensively for lumber and paper pulp, leaving the area cut over and burned except for isolated patches too inaccessible for logging. The present spruce-fir forest covers about 24,000 hectares (60,000 acres). Most of this land is now in public ownership, enjoyed as recreation and a scenic attraction by

millions of visitors to the National Forests, Great Smoky Mountains National Park, Blue Ridge Parkway and Mt. Mitchell State Park.

Fraser fir has long been a local favorite for Christmas wreaths, boughs and trees. By the 1950's, mountain people were beginning to plant trees to meet the increasing demand for such decorations, and soon the Christmas tree industry was developing rapidly. Since 1954, the North Carolina Agricultural Extension Service, North Carolina Division of Forest Resources, and Tennessee Valley Authority have cooperatively assisted and encouraged farmers to plant and culture Fraser fir. The Fraser fir Christmas tree industry has now become an important source of income in the mountain areas of North Carolina, Tennessee and Virginia: over 1,500 growers are involved, and in 1979 it generated $10 million of income in North Carolina (North Carolina Agricultural Extension Service, 1980, personal communication).

Fraser fir is also widely available as an ornamental, and it is grown in the Northeast and Midwest for use as both a yard and Christmas tree. The silvery underside of the needles and overall good form are reasons for its popularity, as well as its relatively rapid growth (6-7 ft. height in 8 years). Good needle-holding qualities make it easy to ship. However, the high demand for Fraser fir is somewhat offset by the expense of growing healthy trees. Of the species grown for Christmas trees, Fraser fir is susceptible to the greatest number of insects and diseases, and scarcity of seed and seedlings make production cost high. It cannot be grown on soils with poor internal drainage because of Phytophtora root rot (Phytophthora spp.) and must be fertilized and sprayed for spider mites, twig aphids and balsam woolly aphid (E. Thor, 1980, personal communication).

Legal Status

Several federal laws direct to some extent the current management of Fraser fir and will also help determine future options as the spruce-fir forests are threatened by the balsam woolly aphid. The most important of these are the Wilderness Act, the National Environmental Policy Act, the National Forest Management Act and the Endangered Species Act. The various State Endangered Species Acts and Plant Pest Laws are also relevant.

A significant portion of the Fraser fir stands are on lands which are (or are being considered as candidates) in the National Wilderness Preservation System. These areas, found on National Forests, National Parks, and National Wildlife Refuges, were established by the Wilderness Act of 1964 to be preserved in their natural state for the use and enjoyment of the public. In 1975, the Eastern Wilderness Act identified the need to add more areas in the Eastern United States: some were designated immediately and others set aside for further study. In Wilderness Areas, natural ecological succession operates as freely as possible and the use of chemicals and cutting of timber is normally prohibited. There are no specific directives for problems caused by introduced pests; however, the Act permits measures necessary in the control of fire, insects and disease subject to such conditions as the Secretary of Agriculture deems desirable (NPS, 1975).

Management of National Parks and Forests is also subject to the National Environmental Policy Act of 1969. This law established a process for systematic, interdisciplinary decision making with input from the public on land use policy. The Renewable Resource Planning Act of 1974 and the National Forest Management Act of 1976 set up further guidelines

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and standards for resource planning in the National Forests, with emphasis on multiple-use and regard for public opinion. The Roadless Area Review and Evaluation (RARE) process of the U. S. Forest Service was a product of these legislative acts, designed to identify roadless, underdeveloped areas that would be the best candidates for inclusion in the National Wilderness Preservation System.

The purpose of the Endangered Species Act of 1973 was "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved to provide a program for the conservation of such endangered species and threatened species...". The term "endangered species" refers to any species in danger of extinction throughout all or a significant portion of its range because of any of the following factors:

(1) Present or threatened destruction, modification or curtailment of its habitat or range
(2) Over-utilization for commercial, sporting, scientific or educational purposes
(3) Disease or predation
(4) Inadequacy of existing regulatory mechanisms
(5) Other natural or manmade factors affecting its continued existence

"Threatened species" are likely to become endangered in the foreseeable future, and "species" includes any subspecies of fish ~~or~~ wildlife or plants. The conservation of such species mandated by the Act means "all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which measures provided pursuant to

the Act are no longer necessary." The law also prohibits any interstate or foreign commerce involving such species (U.S. Fish and Wildlife Service, 1978).

Fraser fir could become classified under this law, particularly if it is not able to regenerate under continued balsam woolly aphid attack. Its taxonomic designation may cause some debate, however, and the prohibition on commerce could cause problems for Christmas tree growers. However, this is unlikely since special permits and regulations can be used where applicable and the law was not intended to cover commercially cultivated plants. The U.S. Forest Service and the National Park Service would be required to institute management programs to conserve and promote Fraser fir on their lands.

The states of Virginia, Tennessee and North Carolina each have laws similar to the Federal Endangered Species Act. In recommendations to the Federal List of Endangered Species, scientists in Tennessee and Virginia have classified Fraser fir as "of special concern" and "threatened", respectively. North Carolina has not designated Fraser fir on its recently revised endangered and threatened plant list.

Inspection and Quarantine

The Christmas tree and nursery industries in North Carolina ship Fraser fir trees all over the United States. To prevent the spread of plant pests, the North Carolina Plant Pest Law is used to enforce a number of regulations relating to nursery commerce. Every person, firm, or corporation buying and reselling nursery stock must register and obtain a dealer's certificate for each location from which plants are sold.

North Carolina Nursery Regulations Pest Control Specialists inspect nursery stock (live trees with roots attached) before shipment is made within or out of state. Cut Christmas trees would not be inspected unless they were included as a regulated article under a specific plant quarantine regulation. All nurseries are inspected by an on-site visit at least once annually, and nurseries more active in commerce are inspected more often.

In the northwestern section of North Carolina, collection of wild plants for commerce is still a common practice. These plants are sold in the nursery trade and are sometimes not distinguishable from nursery grown plants. For this reason, four counties and a portion of a fifth are designated as Collected Plant Regulated Areas, and inspection of all plants is required at the time they leave these designated areas. Thus all Fraser fir seedlings collected on Roan Mountain must be examined and certified.

At present the balsam woolly aphid is listed as a "zero" tolerance pest on nursery stock by the North Carolina Pesticide and Plant Protection Division. This designation requires that all nursery stock when moving in commerce be absolutely free of this pest. Exception is made for the seedlings inspected and certified for movement from Roan Mountain. These are allowed to move only to certain destinations listed on the permit, and growers are requested to spray these plants after planting (H. Singletary, North Carolina Department of Agriculture, Pesticide and Plant Protection Division, 1980, personal communication).

The balsam woolly aphid occurs throughout the general range of Fraser fir and other hosts, except possibly for some locations on the west coast and Canada and some nursery and landscape plantings. It is

hoped that inspection and monitoring of Fraser fir commerce will help prevent the insect from infesting areas where it does not already occur.

One precedent for controlling the spread of the balsam woolly aphid by quarantine is in British Columbia. During the late 1950's the insect became a threat to the forest industry of that area when heavy mortality developed nearby in Vancouver and Washington State. In order to prevent its introduction to the large fir forests of British Columbia, representatives from the Provincial Government, Federal Government and various forest industries prepared quarantine measures in 1965 which included:

(1) Legislation to ban movement of *Abies* seedlings and destroy *Abies* seedling stock in nurseries
(2) A survey of infestation boundaries and damage
(3) A public information program
(4) Expanded research
(5) A voluntary ban imposed by industry on movement of *Abies* logs out of infestation zones, from March to October (Vyse, 1971).

This program has been largely successful. At present, anyone growing *Abies* must have a permit and make treatments for balsam woolly aphid as specified by the government. Trees must be inspected prior to shipping, and the sale of cut Christmas trees and foliage is prohibited from January 31 to November 1 (G. Puritch, 1980, personal communication).

SHORT TERM PROTECTION AND MANAGEMENT

Since most of the Fraser fir forests are located on public lands (see Table 1), options for immediate protection and management of the species are controlled in part by policies and priorities of the responsible agencies. A review of each of these agencies follow in the first section, including a brief statement of general policy, a history of the balsam woolly aphid in areas under their administration and efforts to deal with the problem. The second section is a discussion of several issues relating to protection of present fir stands and assurance of a continuing seed source.

North Carolina Division of Parks and Recreation - Mt. Mitchell State Park

Mt. Mitchell State Park was set aside in 1915 as North Carolina's first state park. Its management objectives are to preserve and protect the natural resources of the area while providing recreation. Approximately 3,000 hectares (7,500 acres) of spruce-fir forest type are located within the Park and on adjacent lands managed by the National Forest. National Park Service, Asheville Watershed and private owners.

The balsam woolly aphid was identified on Mt. Mitchell in 1957; this was its first known location in the Southern Appalachians. A survey conducted in 1958 showed that more than 11,000 trees had been killed and the insect was distributed throughout the host type (Amman, 1966). A quarantine program was considered but the idea was discarded due to difficulties anticipated in inspection and enforcement.

TABLE 1.

IMPACT OF THE BALSAM WOOLLY APHID (BWA) ON FRASER FIR, ITS ACREAGE, AND ITS OWNERSHIP

Location	Date BWA Detected	Date of Oldest "Rot Holtz"	Spruce/Fir[1] Area
			hectares
Mt. Mitchell, N.C.	1955	?	502
State Park			1,514
Pisgah National Forest			348
Asheville Watershed			194
Blue Ridge Parkway			364
Private			2,922
Jonas Ridge Nursery, N.C.	1961	?	
Roan Mountain	1962	1958	
Pisgah National Forest, NC			562
Cherokee National Forest, TN			119 [2]
			681
Blowing Rock Nursery, NC	1962	?	
Mt. Sterling	1963	1958	
Great Smoky Mountain National Park, NC			9,020
Great Smoky Mountain National Park, TN			6,656
			15,676
Grandfather Mountain (private), NC	1963	1959	440
Balsam Mountains, NC	1968	?	5,101
Pisgah National Forest			
Blue Ridge Parkway			
Private			
Great Smoky National Park, NC/TN			Average already included above for GSMNP
Clingmans Dome	1972	?	
Mt. Rogers National Recreation Area, VA	1979	1962	202
TOTAL AREA			25,022 [3] [4] [5]

[1] Average number of trees/Acre = 1,000-1,200

[2] 324 ha of only red spruce on Unaka and Beauty Spot Mt. not included.

[3] The isolated community in Nantahala National Forest not included.
October 22, 1979

[4] Isolated red spruce on Bald Mt. in Ashe Co.

[5] Between 607 and 1012 ha estimated as privately-owned.

Various insecticides were tested on Mt. Mitchell during the late 1950's and early 1960's. The need for safe chemical control was especially critical because a portion of the infested area was in the watershed draining into the State Park reservoir. In 1965 the Park Service was spraying a 120 hectare (300 acre) protection zone along the roadsides with lindane (1, 2, 3, 4, 5, 6,- Hexachlorocyclohexane, or BHC), substituting lime sulphur in watershed areas (USFS, unpublished notes). Treatment of the protection zone continued annually until 1967, then again in 1972 and 1974. Spraying was discontinued when the population levels of balsam woolly aphid declined and a study showed that BHC residues were persisting in the soil (Jackson, Sheets and Moffett, 1974).

Annual surveys with Tanglefoot traps have indicated wide fluctuations in balsam woolly aphid populations: in 1978 more woolly aphids were trapped than ever before, then in 1979 there were fewer than ever (North Carolina Division of Parks and Recreation, 1980, personal communication). Since Tanglefoot trap data are not completely reliable as a census technique, the Park Service has not used this information as basis for a chemical control program. While most of the mature firs in the Mt. Mitchell area have died and there have been severe windthrow problems, dense stands of fir reproduction are now present.

U. S. Forest Service - National Forests in North Carolina

National Forests are managed with multiple use objectives, including commercial forest products, wildlife, recreation and watershed. While they are subject to fewer constraints on management activities than the National Park Service, National Forest administrators have specific

legislative regulations for their management plans and must consider such

done to meet an increasing demand for Fraser fir seeds for Christmas tree growers, and to insure an adequate supply in the event that other sources were destroyed by the balsam woolly aphid. Three hundred trees were marked and subsequently included in the protection zone.

Spraying was discontinued in the seed production area in 1974 after many trees had been lost to windthrow (Ward, 1974). Recently plans have been made to resume spraying in this area and permit vehicular access for cone collection.

In 1971 the National Forest Service designated three areas on Roan Mountain for periodic insecticide treatment, based on accessibility, intensity of visitor use and visibility to the public. These areas are also used by the Christmas tree industry for collection of seeds and seedlings. A protection area of 60 meters (200 ft.) on either side of the road or trail is sprayed with a 1/8% solution of lindane. One of the three areas has been sprayed every year, so each area has been treated every three years. The Asheville Office of the U. S. Forest Service - Forest Insect and Disease Management conducts an annual post-suppression evaluation to determine the effectiveness of the spray program (Johnson, Lambert and Barry, 1980). In 1980 the protection area will be divided into two areas instead of three, and annual treatment will alternate. Forty permanent 1/10 acre plots will be established at regular intervals to monitor woolly aphid activity after insecticide treatment.

National Park Service - Blue Ridge Parkway

The Blue Ridge Parkway is managed by the National Park Service; like the Great Smoky Mountains National Park, its objectives are preservation and recreation. Its forest management responsibilities are mostly limited to the land adjacent to the highway, which includes some nature trails and interpretive centers. Fraser fir is found in three areas along the Parkway: the Moses Cone Memorial Park near Blowing Rock, the Mt. Mitchell

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area and the Beech Gap-Balsam Gap section south of Asheville.

The balsam woolly aphid was spread throughout the Mt. Mitchell area in 1958, and by 1964 the two-acre stand of fir in Moses Cone Park was 80% infested (Ciesla, Lambert and Franklin, 1965). The trees in Moses Cone Park were sprayed with lindane in 1967; others, located in the City of Blowing Rock Watershed, were sprayed with lime sulphur in 1970. Many of these trees were also infected by Annosus root rot, Fomes ammosus (Fr.) Cke. (Affeltranger and Ward, 1970). Mortality in the Mt. Mitchell area of the Parkway was not very noticeable since the firs were mixed with spruce and hardwood. No insecticides were used because of proximity to the Asheville Watershed. The first infestation in the Balsam Mountains along the Parkway was detected in 1970 and the insect has since spread throughout the fir there, causing widespread mortality readily visible from the Parkway. The Park Service has made efforts to educate tourists on the Parkway about the balsam woolly aphid by providing informative pamphlets and by advising personnel of the problem.

National Park Service - Great Smoky Mountains National Park

The largest component of the Southern Appalachian spruce-fir forest type--around 15,200 hectares or 38,000 acres--lies within the Great Smoky Mountains National Park. The National Park Service Organic Act of 1916 states that the fundamental purpose of the National Park is "to conserve the scenery and the natural and historic objects and wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." Thus the management priorities are non-consumptive recreational use and preservation. An additional constraint on the management of the Park

is its designation as an International Biosphere Reserve. These areas were established by UNESCO in 1970 as sites for major ecological research and environmental monitoring programs--baselines against which future change can be measured--as well as for preservation of natural ecosystems and gene pools. According to the 1979 Draft General Mgt. Plan, 89% of the Park is managed as a "Natural Environment-Type 1 subzone." Most of this area is being considered by Congress for inclusion in the National Wilderness Preservation System and is managed accordingly: recreation and management policies are to be transient and non-mechanized except in extreme emergencies.

National Park personnel have been concerned with the balsam woolly aphid since it was first detected on Mt. Sterling in 1963. Attempts were made to contain the infestation by cutting all firs in the infested area, which measured 600 meters long and 150 meters wide. However, ground checks the following year showed that an additional 16 hectares around the original area had become infested (Ciesla, Lambert and Franklin, 1965). After the ineffective cutting program was discontinued, the balsam woolly aphid continued to expand its range, monitored by annual aerial surveys and ground checks by the U. S. Forest Service until 1970. In 1978, infestations were present throughout the entire spruce-fir distribution in the Park (Eagar, 1978).

The National Park policy regarding control of the balsam woolly aphid and management of the infested spruce-fir forests has not been completely established. Preservation of the native resource is a priority; there are precedents for elimination of exotic plants and animals where a negative impact on natives has been demonstrated. The use of insecticides is not absolutely prohibited by any law under which the Park is administered.

U. S. Forest Service - Mt. Rogers

The Mount Rogers National Recreation Area, a part of the Jefferson National Forest in Virginia, is responsible for management of the approximately 200 hectares (500 acres) of Fraser fir on and adjacent to Mount Rogers. The priorities for management were set by Congress when the area was established by the passage of Public Law 89-438 in 1966. They are: 1) Public outdoor recreation benefits, 2) Conservation of scenic, scientific, historic and other values contributing to public enjoyment, and 3) Such management, utilization, and disposal of natural resources as in the Secretary of Agriculture's judgment will promote, or is compatible with, and does not significantly impair the purposes for which the recreation area is established.

According to the recently published Mount Rogers National Recreation Area Final Management Plan and Environmental Impact Statement, the spruce-fir forests fall into two special areas: the Lewis Fork RARE II Area and the Crest Zone, both of which are managed for dispersed recreation (e.g. backpacking, horseback riding). The Lewis Fork area has been recommended to Congress for Wilderness designation, and the management will basically be preservation. The objective for management of the Crest Zone is to retain the alpine character of the area for its aesthetic value, dispersed recreation opportunities and grazing benefits. Basically this is accomplished by grazing supplemented by prescribed burning and occasionally by cutting to control encroaching vegetation. Vehicles are prohibited in the Lewis Fork area and are prohibited in the Crest Zone except for a few management activities (most are done on horseback). According to the management plan, an environmental analysis must be done before any collection of cones and seedlings from the Fraser fir forest can be considered.

Until 1979, no balsam woolly aphid infestations were found on Mount Rogers though regular aerial surveys and ground checks had been made. During that year, however, intensive trapping surveys detected two small infestations on Cabin Ridge. Examination of cross-sections cut from infested trees indicated that the balsam woolly aphid had been present for up to 17 years without causing significant damage (three trees showed top die-back and two were dead). Infestations seemed concentrated on the lower portion of the bole (Lambert, Morgan and Johnson, 1980).

Since the fir on Mount Rogers appeared to tolerate the balsam woolly aphid, insecticides have not been used and will not be used unless the current non-lethal situation should change. The current infestations will be monitored closely by the Asheville office of the U. S. Forest Service, Forest Insect and Disease Management.

In the spring of 1980, a co-operative project between the U. S. Forest Service, the Tennessee Valley Authority, the Virginia Division of Forestry, the Virginia Cooperative Extension Service, the Virginia State Park Service, and others was implemented to establish a Fraser fir seed production area in Grayson Highlands State Park. An Environmental Analysis prepared by the Forest Service resulted in an administrative free use permit to select and transplant up to 300 3' - 6' trees from the Cabin Ridge area of Mount Rogers to the seed production area. The seed production area should be at least a partial solution to providing an adequate Fraser fir seed source especially for use in the local Christmas tree industry. The Forest Service is currently preparing an Environmental Analysis for possible cone and seedling collection (K. Brock, Mt. Rogers National Recreation Area, 1980, personal communication).

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U. S. Forest Service - Research and Forest Insect and Disease Management

In addition to administration of the National Forest system, the U. S. Forest Service is responsible for the Forest Service Research Program and the Co-operative State and Private Forestry Program. The latter program was authorized by the Forest Pest Control Act of 1947 to "detect, evaluate, prevent, retard, suppress or eradicate incipient, potential, or emergency outbreaks of destructive insects or diseases on or threatening all forest lands regardless of ownership." Similar provisions are contained in the Co-operative Forestry Assistance Act of 1978 (U. S. D. A. - F. S., 1980). The activities of Forest Insect and Disease Management include surveys to detect insect and disease outbreaks, evaluation of negative impacts of pests, pest prevention and suppression programs, pilot testing of new materials and methods of suppression, and transfer of information and technology from research to users.

Forest Insect and Disease Management, with a field office in Ashville, North Carolina, has been involved with the balsam woolly aphid since it was first discovered in the Southern Appalachians. Work prior to 1961 was administered by the Southeastern Forest Experiment Station; after 1961 Forest Insect and Disease Management was reorganized to form a separate unit. Researchers with the Experiment Station continued to do entomological studies and develop pesticides. During the first years, pesticide screening tests were conducted and studies were begun on the biology of the insect and its possible control by introduced parasites and predators. Plans were made to monitor infestations closely in hopes of detecting new attacks in time to destroy affected trees and prevent spread. Areas of particular aesthetic importance (such as visitor areas

on Roan Mountain and Mt. Mitchell) were to be protected with insecticides where practical, and species conversion considered elsewhere. For several years annual meetings were held by involved agencies to evaluate current conditions and plans. While the insecticide spray programs were largely successful, other attempts to contain the balsam woolly aphid were not.

Aerial surveys were conducted of the entire host type between 1963 and 1970 by Forest Insect and Disease Management, accompanied by ground checks and trapping in some areas. Annual status reports detailed current infestations and evaluated control programs. During the 1970's, emphasis shifted to the "protection zones": annual reports were made on the status of the balsam woolly aphid on Roan Mountain, with occasional surveys elsewhere. A trapping survey in 1979 led to the discovery of infestations on Mt. Rogers and a permanent monitoring system was established. During 1980, aerial photographs will be made of the entire spruce-fir area in the Southern Appalachians.

The present control project on Roan Mountain is funded completely by Forest Insect and Disease Management, and post-suppression evaluations are conducted annually. They are also co-operating with Forest Service Research (Southeastern Forest Experiment Station) in pilot testing fatty acids for control of balsam woolly aphid. The North Carolina Christmas Tree Association has also assisted in funding pesticide research.

Fire Protection

Fire is normally not a problem in the spruce-fir forest because of the relatively high rainfall and cool temperatures. The hazard resulting from overstory mortality of fir from balsam woolly aphid has not been evaluated. However, increased insolation upon the forest floor will cause

drying there, and the dead firs will provide fuel. A fire destroying fir reproduction would be particularly critical in areas where mature trees were no longer present as seed source. Since most fires are started by people, managers in recreation areas may consider relocating trails and campsites away from areas of dead fir.

Control

Biological. The nature of the forest crop and the relative complexity and stability of the forest environment favor the use of biological controls against forest insect pests. The introduction of parasites, predators and diseases is generally safe, economical and self-perpetuating; it can be particularly important in combating introduced pests whose natural controls have been left behind in their native territories. The balsam woolly aphid is controlled to some extent in Europe by several species of flies and wasps, but it is remarkably free of both parasites and primary diseases in North America. Since *A. piceae* is thought to have reached Western Europe from its native Caucasus only within the past century, the search for its predators has extended into Central Europe.

Several insects native to the Southern Appalachians, including lady beetles, red mites and lacewings, have been observed feeding on the balsam woolly aphid but none have had appreciable effect on the population. During the late 1950's and early 1960's a number of predators were released in infested areas of North Carolina by entomologists of the U. S. Forest Service Southeastern Experiment Station. Subsequent evaluations have shown that *Laricobius erichsonii* definitely became established, and probably *Aphidecta obliterata* as well (Amman and Speers, 1971, and Amman, 1980, personal communication). None of these predators has had any impact

on balsam woolly aphid populations. Introductions of the same and various other predators in eastern Canada and the Pacific Northwest were also disappointing and attempts have been discontinued. Ineffective synchronization of predator-prey life cycles, poor searching ability of predators, the high reproductive capacity of the balsam woolly aphid and the rapid death of the host were factors in the failure of predators as a means of control.

Although at least 10 different species of fungi have been isolated on the balsam woolly aphid, only one--*Fusarium larvorum*--shows evidence of pathogenicity. Its virulence is modified after culture on media, and seems to vary with the vitality of the insect (Smirnoff, 1970). Claydon and Grove (1979) extracted several fungal metabolic products from two strains of *Fusarium larvorum* isolated from widely different hosts and localities. The major metabolites, monocerin and the fusarentin ethers, showed insecticidal activity. The same fungus was observed on balsam woolly aphids in North Carolina and cultured for trial as an insecticide. When applied to tree trunks in combination with NIA, there was a 50% reduction in woolly aphids at all stages of the life cycle (G. Fedde, unpublished paper, Canadian Research Council Meeting, Jan.,1972). *Fusarium* fungi are normally vectored by mites, which may make its use as an insecticide impractical.

Chemical. Various chemical insecticides have been found effective against the balsam woolly aphid, but none have been technically or economically feasible for use over large forested areas. Aerial applications have been ineffective even on crown infestations (Hopewell and Bryant, 1969). Chemical insecticides are useful, however, for small and accessible stands of high value such as ornamentals, seed production areas,

Christmas tree plantations and certain recreation areas. Brower (1947) recommended lime sulphur and nicotine sulphate. During the 1960's the chlorinated hydrocarbon BHC (lindane) was widely used despite evidence of residue remaining in the soil for several years. Persistence of insecticides in spruce-fir soils can be attributed to conditions unfavorable to microbial activity, highly acid soils, cool soil temperatures and now intensity of solar radiation on the forest floor. Movement through the soil, however, is minimal (Jackson et al., 1974). Lindane, the only chemical currently registered for this use, has been placed on the Environmental Protection Agency's Rebuttable Presumption Against Registration list. Other chemicals have been tested in search of an environmentally acceptable substitute. The systemic Furadan (carbofuran) was moderately effective on the overwintering generation but had insufficient residual effect over the summer to kill subsequent generations (Carrow, Puritch and Nigam, 1977). Baygon, diazinon, dursban, permethrin, chlorphyrifos and chlorphyrifos-methyl have been found effective in field tests (Hopewell and Bryant, 1969; Hastings and Barry, 1979).

Fertilization shows promise as a safe means of controlling aphid infestation. In the Pacific Northwest, field and laboratory trials have demonstrated that foliar-applied ammonium nitrate solutions are effective in reducing populations or inhibiting build-up of a new infestation both in the crown and on the stem. Fertilizers appear to operate by altering the nutrient composition of host tissues sufficiently to inhibit the settling of crawlers (Carrow and Graham, 1968). Different compounds of nitrogen had different effects, however: urea and a combination of potassium ammonium nitrate and urea promoted aphid establishment and reproduction, while ammonium nitrate affected both these processes and survival adversely (Carrow and Betts, 1973).

Fatty acids and soaps have recently been 'rediscovered' as insecticides and are particularly attractive because they are safe (consisting of compounds normally found in plants and animals), relatively cheap, biodegradable and low in phytotoxicity. The insecticidal action of fatty acids is not completely understood, but they are known to disrupt the integrity of cell membranes and uncouple oxidative phosphorylation, which is a vital metabolic process. Sucking insects are particularly susceptible to fatty acids and soaps, while flies and beetles (common predators of the balsam woolly aphid) are less so. The fatty acids capric, caprylic and oleic and their corresponding soaps have been found effective, particularly on the adult and crawler stages of the balsam woolly aphid (Puritch, 1975). These compounds are available in Canada for use on ornamentals, and it is expected that they will be registered for similar use in the United States as soon as efficacy research is completed.

Silvicultural. Silvicultural methods of control are less useful in the Southern Appalachians than in other areas where fir is grown commercially. This is partially due to differing management objectives; in addition, the high susceptibility of Fraser fir and rapid spread of the insect make it almost impossible to isolate and remove infested stands in time to prevent new infestations. Cutting operations on Roan Mountain contributed to the dispersal and subsequent spread of the woolly aphid when crawlers were present (Lambert and Ciesla, 1967). Silvicultural manipulation may be more useful as a means of reducing fire hazard and facilitating reproduction than as a direct control (Hay, Eagar and Johnson, 1978).

Detection and Sampling Techniques

Fir damaged sufficiently to show changes in crown color are readily identifiable from the air for both sketch-mapping and aerial photography. Experiments in Newfoundland showed that best results were obtained from photographs of a scale 1:720 on Ektachrome Infared film. Four damage classifications--not infested, light to moderate, severe and dead--could be interpreted from the photographs with 90% accuracy (Bajzak, 1966). Similar results were obtained in an aerial survey of Mt. Mitchell, where fir mortality was determined in terms of dead trees/acre. Equations were also developed to compute an index of fir mortality (Aldrich and Drooz, 1967).

Balsam woolly aphids can be detected as they are dispersed in the egg and crawler stages by using Tanglefoot traps (Lambert and Franklin, 1978; Lambert, Morgan and Johnson, 1980). This technique is particularly useful in areas where the trees are lightly infested and/or not showing damage by changes in crown color. However, failure to pick up aphids on the traps does not mean that none are present in the vicinity.

Sampling woolly aphid populations on the host is difficult because of variability in location and density patterns among different host trees and also on individual trees. It is necessary, however, in monitoring infestations to evaluate the effects of predators, weather, stand and site conditions, host tree quality or insecticides. Amman (1969) developed a sampling method using ½ in. diameter pieces of bark taken from the lower bole. He determined that similar variation could be expected at similar population levels on the entire bole, regardless of height or cardinal direction. Bryant (1976) studied the distribution of woolly aphids in crown infestations of balsam fir and concluded that a

suitable sample unit was a second position node from a secondary branch axis. Sampling on Christmas trees in plantations is somewhat simpler and more reliable, since trees are of uniform size and shape.

Seed and Seedling Supply

The commercial success of Fraser fir as a Christmas tree has resulted in a greatly increased demand for seeds and planting stock: the 1980-estimated future annual demand for planting stock exceeded 10 million transplants (3-2) (North Carolina Agricultural Extension Service, 1980, personal communication). Damage from the balsam woolly aphid has limited the mature natural fir stands available for seed collection to a few privately-owned areas in the Balsam Mountains, Roan Mountain and Mt. Rogers. Collection of plant materials for commercial purposes is prohibited by the National Park Service and the North Carolina Division of Parks and Recreation. The U. S. Forest Service issues permits for removal of seeds and wildlings (5 to 12 inches in height) from Roan Mountain, and arrangements have recently been made for limited planting stock collections on Mt. Rogers. In 1978-9, the number of seedlings removed from Roan Mountain was 751,750; in 1979-80, it increased to 1,000,000 (North Carolina Department of Agriculture, Pesticide and Plant Protection Division, 1980, personal communication). The North Carolina Division of Forestry Resources established a seed production area at the state nursery near Crossnore 15 years ago, and the trees have now begun to produce seed. Seedlings are also grown at the Crossnore state nursery and are made available on a quota basis to North Carolina landowners. The total seed, seedlings and wildlings available from natural stands, seed production areas and nurseries are not adequate to meet present demands in North Carolina, Virginia and Tennessee.

There is some debate as to who is responsible for seed and planting stock production: members of the Christmas tree industry as well as state and federal agencies have made efforts to develop adequate supplies of Fraser fir stock. The National Forests are considering this issue as they assemble their long-range management plan, with input from Christmas tree growers and other members of the public. Since the fir forests on Roan Mountain and Mt. Rogers are also important for recreation, potential conflicts must be considered between seed and wildling collection and other priorities such as protection of endangered plant species and preservation of the natural ecosystem and environmental quality suitable for recreation.

Limited research has been done on establishment of Fraser fir seed production areas or seed orchards. Seed production areas are stands chosen on basis of superior phenotype, then generally upgraded by removal of undesirable trees and cultured for maximum seed production. Some experience was gained with the Roan Mountain seed production area between 1964 and 1974. The soil in the chosen area was thin, underlain by rock, and resulted in a shallow root system for the trees. The stand was thinned to enhance cone production. Without surrounding trees for shelter, the shallow-rooted firs blew down in high winds. This area has since regenerated with a dense stand of young fir, and may be used as a seed production area again in the future (T. Rhyne, North Carolina Division of Forest Resources, 1980, personal communication).

The North Carolina Division of Forest Resources seed production area at Crossnore is also known as a seed orchard, since the trees now producing seed were selected as seedlings and planted specifically for that purpose. Several Christmas tree growers have planted similar seed

production areas, and more will be learned as these trees reach full reproductive maturity at around 30 years of age.

True seed orchards are established by selecting propagules from mature trees (6-8 feet high for Christmas trees) or seed from superior trees in seed production areas. The high value of the seed crop makes it economically feasible to shoose a fairly level site with fertile soil and use such intensive management techniques as fertilization, irrigation and application of pesticides. The trees are isolated to reduce pollination from outside sources, rogued of undesirables and cultivated to produce abundant seed at an early age.

Rooted cuttings would be desirable for establishment of clonal seed orchards as well as for eliminating the need for seed in production of Fraser fir. Thor (1966) found that cuttings from the lower portion of the crown had a rooting percent of 16, while cuttings from the top and middle had rooting percentages of only 8 and 4 respectively. There was no significant relationship between rooting ability and either tree age (between 32 and 65 years old) or the elevation of the collection site. Recent experiments with vegetative propagation of Fraser fir have shown that a high percentage of stem cuttings can be induced to root if they are taken from young trees. Hinsley and Blazick (1980) found that rooting ability decreased with stock plant age: rooting percentage was 92 in cuttings from 5-year old trees, compared with 54% from 12-year olds and 29% from 22-year olds. If this technique becomes cost effective, it may alleviate the shortage of seeds and could also permit cloning of trees with tolerance to balsam woolly aphid and/or desirable Christmas tree characteristics.

Impact Assessment

Since the balsam woolly aphid has been in the Southern Appalachian Mountains for less than forty years, the ecological consequences of its damage to Fraser fir are not yet known. The firs may be able to reproduce and maintain populations of at least young trees, or they may gradually be replaced by other trees, shrubs and/or herbaceous plants. Death of the overstory fir component can cause radical changes in the microclimate of the site, altering species composition and growth patterns of plants and perhaps also affecting populations of such resident animals as deer, red squirrel, and boar. Succession following infestation will also reflect differences in communities resulting from previous disturbance by logging, fire, windthrow, etc. as well as inherent site characteristics such as slope, elevation and aspect. Several studies have investigated the initial phases of these ecological changes.

Boner (1979) sampled uninfested fir and spruce-fir stands in the Great Smoky Mountains National Park to provide a permanent record of their composition and structure in the event that Fraser fir is eliminated. He compared these with stands in the Great Smoky Mountains and the Black Mountains, including Mt. Mitchell, which had been infested for 16 to 20 years. Overstory density and basal area were drastically decreased, as was density of the understory shrubs mountain cranberry (_Vaccinium erythrocarpum_) and hobblebush (_Viburnum alnifolium_) and ground coverage of mosses and ferns. The density of thornless blackberry (_Rubus canadensis_) increased greatly as fir mortality caused openings in the canopy, and subsapling fir densities also increased with the length of time since the

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overstory's death.

Dense growth of fir reproduction and/or blackberry also characterized the vegetation in plots on Mt. Mitchell which were established in 1966 and re-surveyed in 1978 (Witter and Ragenovich, unpublished paper, 23rd Southern Insect Work Conference, August 1978). In this study, three one-acre survey areas were established in each of three forest types--pure fir, spruce-fir, and spruce-fir-hardwood--in which the fir had suffered balsam woolly aphid attack. The 1966 tally of trees by species and size class showed that fir mortality had reached 98%, 95% and 81% in the spruce fir, spruce-fir-hardwood and fir types, respectively. By 1978, some areas were almost completely leveled by blowdowns and the community structure of all areas was altered. The 1978 data have not yet been analyzed.

Mt. Sterling in the Great Smoky Mountains National Park is another area with a relatively long history of balsam woolly aphid infestation. Upon discovering the insect there in 1963, the National Park Service decided to remove all fir trees in buffer strips to isolate the infestations. By 1967, after approximately 54,000 trees of various sizes had been cut, this control effort was discontinued because it had clearly failed to contain the infestation and the balsam woolly aphid eventually killed all but a few of the firs. In 1977, a comparison was made of the residual canopies and developing understories of the cut and uncut areas (Hay, R. L., unpublished). Analysis of size class and species composition showed that Fraser fir was the most abundant understory tree species in both the cut and uncut areas, comprising 84% and 78%, respectively. The fir reproduction tended to be larger in the cut areas, and ground coverage by mosses was more extensive there. The uncut areas were characterized by a greater abundance of ferns and more vigorous growth of shrubs (Sambucus, Rubus and Vaccinium).

In 1959 and 1962, permanent plots were established in the high altitude forests of the Great Smoky Mountains National Park to inventory vegetation as a baseline for monitoring future change (Becking and Olson, 1978). When these plots were resurveyed in 1976, only one of these plots had been significantly affected by the balsam woolly aphid. In this area extremely dense fir reproduction had developed in the openings caused by death of the overstory trees, and an increase in *Vaccinium erythrocarpum*, *Rubus canadensis*, *Betula alleghaniensis* and *Sorbus americana* was also noted. This dense understory caused a reduction in abundance of ferns and an increase in mosses. The spruce overstory increased in basal area as their diameter growth responded to release from competition by mature fir trees.

Fraser fir mortality will also affect succession on the grassy balds, where tree species have been encroaching for over 30 years. It is predicted that if the present rate of tree invasion continues, all the balds in the Great Smoky Mountains will be covered by forest within 30 to 70 years (Lindsay and Bratton, 1980). If the fir are killed, however, the high elevation balds may be covered with either very young trees or rhododendron. A forest of birch, beech, serviceberry and spruce could form the final stage of succession, but encroachment would be much slower than if healthy firs were present.

Each of these studies assessing the impact of balsam woolly aphid infestation conclude that healthy reproduction of Fraser fir is abundant, though the future of these young stands is uncertain. Continued monitoring of permanent plots in the spruce-fir forests will provide information on the environmental and community changes as succession proceeds and the Fraser fir and balsam woolly aphid continue to interact. A partial listing

of such plots follows, along with the responsible agencies.

1) 82 plots established by R. H. Whittaker and R. W. Becking between 1959 and 1961, in the Great Smoky Mountains National Park. National Park Service.
2) 12 plots established in 1966 by J. A. Witter in Mt. Mitchell State Park, North Carolina. U. S. Forest Service-Forest Insect and Disease Management, Asheville Field Office.
3) 131 plots established in 1976 and 1977 by K. D. Johnson and C. C. Eager, in the Great Smoky Mountains National Park. University of Tennessee and National Park Service.
4) The National Park Service is in the process of establishing a network of permanent plots in the Great Smoky Mountains National Park for vegetation mapping and baseline data to monitor future changes. Eventually there will be around 600 plots; at present there are 10 in the spruce-fir. National Park Service.

Management of Balsam Woolly Aphid--Infested Forests

As assessment of balsam woolly aphid impact becomes more complete, management decisions can be made on basis of that information. Foresters in Maritime Canada have established that they can expect alternating periods of damage and recovery, and have adjusted their management of balsam fir to include a process of site hazard rating, thinning and fertilizing to shorten the rotation period, salvage and species conversion (Schooley and Bryant, 1978). The situation in the Southern Appalachians, of course, is quite different: damage of Fraser fir is much more severe than that of balsam fir, and the fir forests here are managed for preservation and recreation instead of for pulpwood and lumber.

While very little research has been done on Fraser fir silviculture,

a number of observations made in natural stands could be applied as techniques to favor its reproduction and growth. Since seedlings and saplings are generally abundant even in areas of severe woolly aphid damage, release of this understory by removal of dead and dying mature trees would be beneficial. Fraser fir responds well to release, and is able to thrive in full sunlight. Partial release may be best in some cases, but total release works well if seedlings have developed roots in mineral soil (seedlings rooted in the humus layers after release will die during periods of moisture stress). Dense, even-aged stands of Fraser fir would result from removal of the overstory in stands carefully selected according to understory species composition and stage of development. If these stands could survive until seed bearing age--between 15 and 20 years--then fir could be perpetuated in natural stands (Hay, Eagar and Johnson, 1978).

Seed production might be enhanced by thinning, since crown release and subsequent growth in remaining trees increases both loci for cone production and the energy necessary for cone maturation. Fraser fir is a prolific seed producer, with good seed crops occurring every 2 to 4 years and light crops in the intervening years. Wind will dissiminate seeds up to 180 meters. The effective distance is much less, however, and many seeds falling with cone scales land close to the base of the tree (USDA, 1965).

Species conversion or planting of genetically resistant or tolerant Fraser fir may be other options. At present, very little is known about the mechanisms of resistance to balsam woolly aphid attack. A few isolated trees in the Great Smoky Mountains, Mt. Mitchell, and Roan Mountain have been observed to withstand heavy attack, with insect populations building up, then declining and apparently not harming the host. On Mt. Rogers,

Virginia, infestations covering several acres were dated to 1962; the trees, however, have suffered very little damage. It has been suggested that these trees are not Fraser fir but instead the more aphid-tolerant bracted balsam fir, or a hybrid between the two (Lambert, Morgan and Johnson, 1980).

Balsam Woolly Aphid Biology

Taxonomy. *Adelges piceae* belongs to the insect order Hemoptera (Hemiptera) family Phylloxeridae (Chermidae, Psyllidae or Jumping plant-lice), superfamily Aphidoidea and sub-family Adelginae.

Life Cycle. Members of the Adelginae sub-family exhibit complex polymorphic life cycles which often include alternation of hosts, with spruce (*Picea* spp.) being the primary host and the true firs (*Abies* spp.) being the secondary host. Sexual reproduction is associated with the primary host and parthenogenesis with the secondary host. *Adelges piceae* is an exule form capable of maturing and reproducing parthenogentically, thus maintaining its population exclusively on the fir hosts.

The functional life cycle of the balsam woolly aphid consists of an egg stage, three larval instars and the adult. The following descriptions of each stage are based on examinations made in Eastern Canada by Balch (1952).

1) Eggs laid by the stationary parent are attached to the bark by a silken thread. They are oval and about 0.4 mm. long. Initially light amber-colored, the egg becomes orange-brown as the embryo develops. Young larvae emerge head first from the end opposite attachment.

2) The first instar (neosisten) is the only form capable of initiating movement. The 'crawlers' are about 0.4 mm long with an oval, vertically flattened body. Once a suitable feeding site is located, the stylet (a slender, thread-like mouthpart used for feeding) is inserted into the bark. The insects light purple color then darkens gradually, small tufts of waxy threads appear on its side and its legs and antennae begin to atrophy. It will remain at this location for the remainder of its life, though the stylet may be removed and reinserted. A dormant period of at least 3 weeks precedes the first moult.

3) The second instar develops after the first moult; its body is broader, longer (about 0.5 mm) and becomes covered with long, curling waxy threads.

4) The third instar is about 0.65 mm in length.

5) Adults are about 0.8 mm long, hemispherically shaped and covered with 'wool'. Since these insects tend to congregate, the wool forms a dense protective covering and make infestations readily visible. All adults are female. Reproduction begins within 3 days of maturity and continues for around 5 weeks.

Seasonal Chronology. Balsam woolly aphid populations in North America are capable of producing a minimum of two generations a year, and Amman (1962) found that three generations could reach maturity in North Carolina. The first generation, known as the hiemosistens, overwinters in the first instar stage while the morphologically similar aestivosistens completes its life cycle during the summer.

In general, only those first instars which have inserted their stylets

and become dormant are able to survive the winter months. Feeding activity begins when the host tree starts its annual growth cycle in the spring and is indicated by a swelling of the insect's body and a small, clear drop of honeydew at the anus. All larvae do not break dormancy simultaneously, however: vigorous host trees are usually the first to initiate spring growth and Balch (1952) observed 20 days variation between individual insects in breaking dormancy on the same tree. In North Carolina, Amman (1962) found that feeding during the 1960 season began as early as April 10 and as late as May 15. Adults of the hiemosistens generation were most numerous around mid-May, and those of the following aestivosistens peak in mid-August.

Metamorphosis of the balsam woolly aphid is influenced by such environmental factors as light, temperature and moisture as well as condition of the host tree. The duration of the incubation period (around 10 days) and the first instar's dormant diapause are both lightly variable. This developmental flexibility allows the insect to infest hosts over a wide range of climatic zones and to adjust to local weather extremes. A portion of the population can break dormancy early and develop rapidly if conditions are favorable, thereby increasing the number of generations per year. If early development of some individuals should occur during unfavorable conditions, the slower developing portion of the population can maintain the infestation.

Population Dynamics. Factors limiting the distribution and abundance of the balsam woolly aphid include the insects' reproductive potential, environmental conditions, and the carrying capacity of the host tree.

Mortality due to climatic factors may be high occasionally, particularly

to the egg stage, but they do not provide an effective limit to population growth (Balch, 1952). The lethal minimum temperature is -34°C for overwintering first instars and 0°C for all other stages. Amman (1970) reported that an overnight temperature of -34°C on Mt. Mitchell, North Carolina, caused higher than normal mortality but there was no indication that significant control of aphid populations would result from these rare low temperatures in the Southern Appalachians. Low temperatures during the summer increase incubation time.

High ambient air temperatures are not fatal and can in fact speed the rate of development throughout the insects' life cycle. High temperature at the bark surface, particularly in combination with low humidity, can cause dessication fatal to the adult and all nymphal stages. Heavy rains may mat the wool and lead to subsequent dessication, but neither rain nor heavy fog will 'drown' aphids. Protection from the weather is provided by the wool itself, the shade of the tree crown, and by the insects' habit of congregating on the undersides of twigs, branches, mosses and lichens and in bark crevices and lenticels (Balch, 1952).

Reproductive rates are influenced by weather conditions throughout the life cycle, the vigor of the host tree, the amount of protection provided at the feeding site, and genetic factors. Balch (1952) reported that the hiemosistens averaged about 100 eggs per adult with a maximum of 250, while the aestivosistens averaged about 50 eggs per adult with a maximum of 105 eggs. With a 60% rate of survival for both generations, the annual population multiplication averages about X 5000.

A greater proportion of the winter generation survive environmental stresses than of the summer. Amman (1970) observed that during the initial

period of outbreak in a stand, increased insect population density appeared to result in increased fertility. Later there was a strong inverse relation between adult density and fertility, probably due to competition for food at peak densities. Thus survival and reproduction were best on trees with less than extremely dense populations of aphids.

Balsam woolly aphids in North America are free of parasites, predators and diseases capable of limiting its population. In the absence of other controlling factors, the upper limit of the population must be determined by intraspecific competition and starvation. Since heavy infestations usually cause rapid and severe damage to the host tree, its carrying capacity is quickly surpassed. The aphid population then drops sharply and the tree dies.

Behavior. The balsam woolly aphid is wingless and capable of independent movement only during the first instar or crawler stage, when it actively seeks a feeding site. Both eggs and crawlers, however, are passively dispersed over long distances by wind. Balch (1952) found that they were transported more than 90 meters by surface winds and several kilometers by vertical air currents; Amman (1966) reported wind dissemination over 68 kilometers in the Southern Appalachian Mountains. Wind and accidental transport by humans are primarily responsible for the spread of the balsam woolly aphid across the great distances separating the spruce-fir regions in the East.

Within a stand having a relatively closed canopy, the movement of crawlers is from crown-to-crown or from crown-to-stem, but rarely from stem-to-stem (Greenbank, 1970). Crawlers falling from above infest seedlings and saplings. Atkins and Hall (1969) observed that environmental conditions (e.g. light intensity and higher temperatures) may facilitate

insect development on trees at the edges of stands and the accessibility of such infestations to wind currents suggests that such areas could be important for long distance dispersal by wind.

Crawlers are capable of moving 90 meters or more and can remain active for at least eight days without feeding (Balch, 1952). However, most settle near their parent within two or three hours of hatching. Larval mobility is more important for movement on the host tree than for dispersal of populations. Distribution on a given host depends upon available light, gravity, accessibility of young, tender parenchyma at wounds, lenticels and crevices, and feeding areas stimulated by other larvae.

The initial locus of infestation by wind-transported aphids would seem to be primarily a matter of chance, although Amman (1970) observed that it usually began near mid-height on the tree trunk. This varies with tree height and age: on older trees with rough bark along entire stem the infestation starts higher in the tree, while on younger trees the infestation often begins near the base where the rougher bark is usually located. The selection of a certain height on the bole is probably a result of the crawlers' tendency to settle in moderately intense light (Balch, 1952) and thus varies with stand conditions, though bark thickness and texture also seem to be important. In any case, the crawlers appear capable of locating preferred feeding sites. Atkins (1972) observed that groups of crawlers tended to settle more quickly than isolated individuals.

The stylet of the crawler penetrates the bark between cells (aided by a dissolving action of the saliva on the middle lamella), passing through the phellem into the phelloderm where the insect feeds in cortical parenchyma. Nerves at the base of the stylet provide a tactile sense: obstructions can be felt, the absence of satisfactory food detected, and relocation of the

stylet prompted. The stylet may be partially withdrawn and reinserted, but the insect remains stationary. Prior to entering diapause, a salivary substance is secreted from the tip of the maxillae to form a sheath around the stylet. Following the diapause period, the larva begins to feed and secrete the salivary substance, which modifies the feeding site to facilitate nutrient uptake (Balch et al., 1964).

The balsam woolly aphid is so small that chemical assay of its saliva is very difficult, and it has never been successfully reared in laboratory culture. Thus its feeding mechanisms and nutritional requirements are not known in detail. The enzyme pectinase, isolated in the saliva of related insects, aids in intercellular penetration by hydrolytic action. Other enzymes and metabolites, as well as amino acids, 3-indoleacetic acid (IAA) and gibberellic acid, are probably also constituents of woolly aphid saliva (Mullick, 1977). In studies involving European silver fir (A. alba), Kloft (1957) observed close relations between aphid density and the amount of active protein in the feeding area of the bark. Reactions in the host cells caused by salivary secretions and feeding activity apparently increase tissue metabolism and storage of soluble nitrogenous constituents in cells adjacent to the stylet. This in turn increases fecundity and survival and accelerates development of the insects. It may also explain why they tend to settle in groups.

The occurrence of juvabione-related compounds in infested Abies has been investigated, but no certain relationships were found. These chemicals can act as juvenile hormone analogues. Aphid development may also be affected by abnormal hormonal interaction caused by the concentration of these compounds in the infested bark (Puritch and Nijholt, 1974).

Host Pest Interactions

The balsam woolly aphid is an obligate parasite on Fraser fir, obtaining food and shelter in amounts dependent upon the hosts capacity to provide them. Some trees provide conditions more favorable to the establishment and multiplication of the insect than others, e.g., external bark characteristics and feeding conditions within the bark tissues. Such qualities can be influenced by genetics, modified by the environment and/or related to size, age and physiological condition of the tree (Balch, 1952). Different fir species and individuals also differ in their reaction to attack.

With continued infestation development, host trees display characteristic reaction patterns. These help to explain how the insect injures the tree and they also provide an index to the amount of damage already sustained. Tree reactions may be divided into two categories--microscopic symptoms that concern cell and tissue changes, and macroscopic symptoms that are readily observed in the tree.

Microscopic Changes.

Microscopic tissue changes in response to balsam woolly aphid attack are quite similar in all *Abies*; the differences exist mainly in the rate and degree of change. Damage develops both from physical injury by insertion of stylets and also from chemically-induced injury produced by salivary injections. The latter is by far the more important because the secretions either directly or indirectly change the balance of growth hormones and inhibitors in the host, causing abnormal development of wood and bark tissues (Balch et al., 1964).

In the bark layer, a substance contained in the saliva (or produced in the host tissues by action of the saliva) diffuses from the point of

insertion and causes parenchyma cells contiguous to the stylet tracks to increase in number and size. This is accompanied by an enlargement of the nuclei and thickening of cell walls, producing cells up to seven times larger than normal. Neighboring cells later proliferate and form a secondary periderm, a necrophylactic periderm which is a part of the normal wound-healing process in all instances of wounding (Mullick and Jensen, 1973). Mullick (1975) identified a non-suberized impervious tissue (NIT), the development of which is prerequisite to formation of the necrophylactic periderm. He observed that in susceptible response to balsam woolly aphid attack, the NIT and therefore the necrophylactic periderm may form either partially or not at all. European firs are apparently able to complete this process rapidly enough to isolate affected tissues and thus tolerate woolly aphid attack. Some North American firs, notably white fir (Abies concolor Gord. and Glendl.) and noble fir (Abies procera Rehd.) exhibit this capacity. Because of the energy and nutrients necessary for the wound-healing process, overall tree vigor is an important factor in the ability to withstand infestation (Bryant, 1974). Water stress greatly affects the formation of NIT; consequently the water balance of the tree at the time of damage plays a major role in its ability to heal and recover. Infestations on dry site trees or during periods of drought would thus be more damaging (Puritch and Mullick, 1975). The balsam woolly aphid's characteristic effect of interfering with translocation--causing water stress--and of reducing tree vigor makes the host less able to resist attack.

The salivary secretion also affects the xylem. The cambium is stimulated to produce a local enlargement of the xylem ring, extending biaspetally from the point of injection. The tracheids of this wood

have thickened, irregularly shaped cell walls and dark, brittle cellulose. They are histologically similar to those of compression wood: secondary walls are marked with checks, cells are highly lignified, short, and thick-walled with a thick lumen. This abnormal wood is called 'rotholtz' or 'redwood' because of its reddish color (Doerkson and Mitchell, 1965). Balch, et al. (1964) found that these effects on the xylem could be duplicated by application of the auxin 3-indoleacetic acid (IAA). Apparently the saliva contains something that causes an abnormal concentration of a growth substance having properties similar to IAA.

Experiments involving an acidic growth inhibitor known as beta-inhibitor have helped to further explain the disruption in cellular processes caused by the balsam woolly aphid. Beta-inhibitor is found in the bark of healthy balsam fir, but is abnormally abundant in woolly aphid-infested trees. It acts selectively to inhibit formation of new vascular cambium and phellogen without inhibiting the proliferation of cells forming the undifferentiated parenchyma tissue. When low beta-inhibitor concentrations were applied to bark in tissue culture, parenchyma tissue developed and persisted; at high concentrations the tissue was produced but later died and disappeared. Hypertrophy of phloem parenchyma and ray cells seemed to be caused by over-optimal content of beta-inhibitor in the phloem. This hypertrophy disrupts nutrient flow to the undifferentiated parenchyma tissue. A similar sequence occurs when the balsam woolly aphid feeds: swelling due to hypertrophy and hyperplasia in cortical phloem tissues leads to death in tissues distal to the swollen region (Bonga and Clark, 1965).

The reaction of the cambium in producing 'redwood'is dependent upon the vigor of the tree and intensity of infestation. Balch, et al. (1964)

observed that maximum stimulation occurs in vigorous trees that are only moderately infested, with heavy infestations tending to inhibit growth. This suggests that the salivary substance is toxic at high concentrations and the growth responses depend upon a reaction or interaction with some factor in the tree that varies with its vigor. The presence of 'redwood' is useful in determining the chronology of infestations on individual trees, as it shows up plainly in cross-sections. It may, however, be confused with compression wood and does not consistently occur on infested trees. Puritch and Johnson (1971) found that on grand fir (Abies grandis (Dougl.)Lindl.) a premature heartwood having occluded pit membranes was formed instead.

The movement of water through both 'redwood' and premature heartwood is drastically reduced, and tissues distal to the affected xylem usually die (Puritch, 1971). In the bark layers, the proliferation of abnormal cells interferes with translocation in phloem sieve cells, producing a girdling effect. As fluid movement is impaired, photosynthesis and respiration are reduced (Puritch, 1973). These factors combine to cause the death of the host tree.

Macroscopic Changes. Effects of aphid attack that are outwardly apparent are more variable among host species than are the microscopic tissue changes. Infestations are usually described as stem attack or crown attack, depending on where the aphid population is concentrated. Greenbank (1970) suggested that the type of attack is influenced more by climate than by host species characteristics: on balsam fir in eastern Canada stem attack is more common in continental climatic zones and crown attack is more common in maritime zones. The bracted balsam fir of Virginia usually suffers crown attack; stem attack is much more

prevalent on Fraser fir although small suppressed trees and reproduction can develop crown infestations as insects drop onto them from above (Amman and Talerico, 1967). In the Pacific Northwest, Mitchell (1966) found that the character and effects of infestation differed markedly on the three host species. Grand fir is subject to stem infestations but is the most resistant species, capable of withstanding attack for up to 15 years. Probably no more than 30% of the infested trees die. Pacific silver fir (Abies amabilis [Dougl.] Forbes) is more likely to suffer crown attack, though stem attacks also occur and can kill the trees within 3 or 4 years. Subalpine fir is the most sensitive of the three northwestern hosts; it is highly susceptible to stem attack, with up to 90% of infested trees dying within 5 years. Infestations on grand fir are usually concentrated at the base of the trunk, while subalpine fir is usually attacked higher on the stem. Since more rings actively conduct water at the base than higher up on the stem, a given amount of aphid infestation at the base would be less damaging than the same amount higher up. This may account for grand fir's relative tolerance (Mitchell, 1967). The apparently tolerant firs on Mt. Rogers, Virginia, also have infestations concentrated near the base of the tree. Geographic and site factors were also important influences on infestation characteristics in the Pacific Northwest.

Crown infestations are characterized by gouting or swelling at the nodes followed by deformation of shoots and internodes, down-curling branches, tip inhibition and dieback. Appreciable mortality does not occur until 10 to 20 years after initial attack, and recovery is possible (Bryant, 1970).

Stem infestations cause death quite rapidly, often within a few years of initial attack, because of the direct translocation impairment. This

type of attack is evidenced by wool spots on the stem and change of foliage color from the normal healthy green to a faded yellow-green, then bright rusty red and finally brown. This sequence may be altered by the severity of attack, host tolerance, and water stress or other environmental conditions. There is also a decrease in production of new needles. Amman (1970) observed the following infestation pattern on Fraser fir:

1) Increased diameter growth at the time of initial attack
2) Increased aphid survival as the bark is changed by feeding
3) Peak aphid population, with insect survival closely related to tree condition
4) Decline in aphid survival and also tree growth
5) Disappearance of aphids, and
6) Death of the host

Other effects of balsam woolly aphid attack include reduced reproductive potential and increased susceptibility to further damage by other organisms. Fedde (1973a) observed that the association between aphid attack on Fraser fir and damage to the seed crop appeared to be linked to cumulative injury sustained by the tree rather than to the level of infestation in the year cones are produced. He found that seeds produced by infested trees were smaller (25% less than normal in length), lighter, less viable (32% germination as compared to a normal 75%) and more susceptible to attack by the chalcid Megastigmus specularis (Walley) (28% more were destroyed). The frequency of chalcid attack increased as the woolly aphid infestations became more severe, as did losses due to empty seeds and failure of embryos to develop. Cone production was decreased and limited to the upper third of the crown (Fedde, 1973b).

In contrast, Schooley (1976) found no appreciable reduction in the number, size of cones or quantity of seeds produced by invested balsam fir. This suggests that the girdling effect of stem attack on Fraser fir has a more pronounced impact on reproductive functions than the crown attack on balsam fir.

As the physiological processes of the host are altered by balsam woolly aphid infestation, resistance to further damage by disease organisms and other insect species is decreased. Hudak and Wells (1974) found a positive correlation between the level of aphid damage and the incidence of root rot caused by *Armillaria mellea* (Vahl ex Fr.). The percentage of infected roots, the length of mycelial fans on infected roots and the average percentage of root circumference covered by mycelium increased as aphid damage increased from light to severe. The fungus destroys the cambium and phloem of the roots and root collar and reduces the concentration of most macro-nutrients. Thus *A. mellea*, common throughout eastern North America, may be a factor contributing to mortality of trees infested by balsam woolly aphid. The bark fungus *Lachinellula agassizii* was observed on heavily infested, green crowned Fraser fir which subsequently died (Fedde, 1974).

Weakened trees are often attacked by bark beetles, wood wasps and other wood boring insects, which also may introduce fungal pathogens. The role of these secondary attacks in the decadence and mortality of firs attacked by balsam woolly aphid has not been studied in detail (Schooley and Bryant, 1978). Damaged and weakened trees are also more susceptible to windthrow and top breakage, which is a significant factor in many fir forests of the Southern Appalachians due to exposure to high winds and temperature extremes. The dead trees constitute a fire hazard

to those still living.

Host Susceptibility. There is considerable evidence that balsam woolly aphid infestations on a given fir species are influenced by characteristics of the individual tree (e.g. bark morphology, size, growth rate), climate, site, and community. While Fraser fir is in general highly susceptible to infestation, the differing responses that have been observed may provide information useful in predicting the future status of the host.

Working with Fraser fir in the Great Smoky Mountains, Johnson (1977) found that tree size was an important factor in determining suitability as a host and also the amount of damage likely to be sustained. She observed that trees supporting the heaviest populations of aphids were dominants and co-dominants with relatively large mean height and diameter. Mortality, however, was more rapid on the smaller, suppressed trees. Balch (1952), and Johnson, et al. (1963) also found that on balsam fir in newly infested areas, the insect first became numerous on the larger trees. These observations suggest that large size increases the probability of intercepting the air-borne aphids, thereby causing these trees to be the first in the stand to become infested. This additional time could permit the development of infestations more severe than those on smaller trees. Larger trees also have more rapid growth, and tree vigor seems to favor multiplication of the insect (Balch, 1952). Amman (1970) found that when the maximum number of aphids observed was compared to growth of trees in the year just prior to infestation, the fastest growing trees supported the densest populations.

Johnson (1977) found no clear relation between either tree age or bark characteristics and aphid population levels. However, Greenbank

(1970) and Amman (1970) reported that infestations were more severe on rough-barked trees than on those with smooth bark, and suggested that crevices and lenticels provided protection for the insects. A moderate cover of moss and lichen is most favorable to aphid establishment and survival: trees with no epiphytes provide less protection, while a heavy matt prevents penetration (Johnson, 1977).

Site characteristics such as soil type and texture, moisture, elevation and aspect are also relevant to aphid infestation. They may affect the insect population directly by determining accessibility and microclimate, or indirectly influencing the growth and vigor of the host tree.

In the Pacific Northwest, Mitchell (1966), Johnson, et al. (1963) and Harris (1973) found that aphid populations were usually high on sites with a high site index. Brower (1942) reported that in Maine the infestations on balsam fir were most severe on those trees growing on poor sites with low-lying, poorly drained soils. Balch (1952) could find no conclusive relationship between forest type, site quality and degree of infestation or damage in eastern Canada. In Newfoundland, damage was more severe on dry sites than on moist sites (Bryant, 1974). Spruce-fir forests in the Southern Appalachians do not have the marked variety of habitat found elsewhere in North America and site indices have not been developed. Topographic factors, however, are relevant to site quality through influence on temperature, soil properties, water balance and insolation. Johnson (1977) found that in the Great Smoky Mountains stands having the highest percentage of infestation were on south-facing slopes. The impact of preceding dry summers was particularly pronounced on southern exposed sites; since the woolly aphid impairs the trees fluid

translocation system, trees on these sites may suffer more damage. Warmer temperatures would also facilitate insect development and reproduction. Community structure may also be a factor. Eagar (1978) observed that young, dense, even-aged stands of predominantly Fraser fir were less susceptible to attack than older, more open stands.

Christmas tree plantations provide an environment much different from that of the natural stands, and are found at lower elevations. There has been no research evaluating the effects of these different conditions on the life cycle, survival or infestation patterns of the balsam woolly aphid.

Infestation Patterns. Research involving different geographic localities and host species have shown that susceptibility (probability of attack) and degree of infestation (severity of attack) vary among and within fir stands, sometimes producing patterns. Climatic factors are critical in determining the rate at which the insect population reaches outbreak proportions and spreads, as well as regional patterns of dispersal. The ultimate level of the population is dependent upon biotic factors, particularly those properties of host trees relevant to their suitability as food and shelter for the wolly aphid (Balch, 1952, and Greenbank, 1970). Eager (1978) reported a pattern of infestation spread on peaks in the Great Smoky Mountains from lower to higher elevations. The initial infestations found along the northern hardwood-fir ecotones were small, numerous and scattered. As these expanded and merged, large infestations developed and convective winds disseminated the insects upslope. A similar pattern was observed on Roan Mountain and Grandfather Mountain (Ciesla, Lambert and Franklin, 1965). Within individual stands, the large, dominant trees became infested first and may maintain heavy populations for several years before succumbing. Smaller trees may be

infested later, but they die relatively quickly (Johnson, 1977; Amman, 1970).

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